ZOOLOGIA 38: e63231
ISSN 1984-4689 (online)
zoologia.pensoft.net

RESEARCH ARTICLE

Temporal and spatial segregation of top predators (Felidae) in a Mexican tropical Biosphere Reserve

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ABSTRACT. Jaguars, *Panthera onca* (Linnaeus, 1758), and pumas, *Puma concolor* (Linnaeus, 1771) are the largest felids in the neotropics. Both can overlap in niche axes (time, space and prey), and are therefore potentially competing species. Segregation mechanisms presented by a low overlap in one of these axes of niche can facilitate the coexistence. Our aim was to analyze jaguar and puma temporal and spatial overlap for understanding their segregation mechanisms. Between 2015 and 2017, twenty-six camera trap stations were located in five habitat types of El Cielo Biosphere Reserve (ECBR) in northeastern Mexico. Temporal activity was analyzed using circular statistics and time overlap analysis. Spatial overlap was calculated with the Pianka index and a selectivity habitat analysis. Our results showed that jaguars and pumas were nocturnal and that the temporal overlap was high (Δ_4 = 0.77). We found an intermediate spatial overlap (Pianka index = 0.61). Jaguars were more selective and preferred the deciduous forest. In comparison, pumas preferred oak-pine forest, but also used oak and deciduous forest. Our results indicate that spatial segregation best explains the coexistence of jaguars and pumas in our study area, probably due to both habitat diversity in the reserve and the generalist habits of the puma.

KEYWORDS. Camera trap, coexistence, El Cielo Biosphere Reserve, northeastern Mexico, *Panthera onca*, *Puma concolor*.

INTRODUCTION

Activity patterns and habitat use are important components that describe the ecology and behavior of species and may facilitate coexistence between species or individuals that experience intra-guild competition (Gause 1932, Hardin 1960, Fedriani et al. 1999, Karanth and Sunquist 2000, Harmsen et al. 2009). Top predators that have similar morphology, food habits, distribution, and life history can develop mechanisms of segregation in their use of the three main ecological niche axes (temporal, spatial, and trophic) to ensure their coexistence (Schoener 1974, Pianka 1978, Di Bitetti et al. 2010, Morato et al. 2016, Rayan and Linkie 2016). In a community where species make discriminate use of resources (time, space, and food) while avoiding overlap, each species could have exclusive access to time, space, or food, thereby reducing the risk of direct encounters and competition (Carothers and Jaksić 1984, Castro-Arellano et al. 2010, Romero-Muñoz et al. 2010, Gómez-Ortiz et al. 2015). As such, species with intra-guild competition potential provide a useful focal group to understand the mechanisms of segregation that allow their coexistence (Hearn et al. 2018).

Jaguars, *Panthera onca* (Linnaeus, 1758), and pumas, *Puma concolor* (Linnaeus, 1771), constitute a large mammalian predator guild that can affect the structure and pattern of associated ecological communities (Miller et al. 2001, Sunquist and Sunquist 2002). They also are the largest felids in the Neotropics and are sympatric top predators across the entire jaguar range in Central and South America (Iriarte et al. 1990, Sunquist and Sunquist

2002, Haines 2006). Jaguars are considered an endangered species in Mexico (SEMARNAT 2010). Both species can overlap in temporal activity, habitat use, and prey species consumed (Núñez et al. 2000, Scognamillo et al. 2003, Romero-Muñoz et al. 2010). Thus, they potentially can compete with each other and represent suitable subjects for the study on segregation strategies.

Some authors suggest that competition between jaguars and pumas is low due to differences in diet (Aranda and Sánchez-Cordero 1996, Núñez et al. 2000, Novack et al. 2005, Cascelli de Azevedo and Murray 2007, Flores-Turdera et al. 2021), temporal (Harmsen et al. 2009, Romero-Muñoz et al. 2010), and spatial segregation (Scognamillo et al. 2003).

Generally, jaguars consume larger prey than pumas, and pumas have a more diverse diet (Iriarte et al. 1990, Polisar et al. 2003, Scognamillo et al. 2003, Flores-Turdera et al. 2021) and can easily switch to other prey when their primary prey population density falls (Soria-Díaz et al. 2018). Studies on the temporal activity of jaguars show they are nocturnal in some places of their distribution (Rabinowitz and Nothingham 1986, Emmons 1987, Núñez et al. 2002, Maffei et al. 2004, Di Bitteti et al. 2010). Pumas tend to be active in crepuscular (dawn and dusk) and daylight hours (Di Bitteti et al. 2010, Hernández-SaintMartín et al. 2013, Ávila-Nájera et al. 2016, De la Torre et al. 2017). Jaguars are considered habitat specialists; they prefer dense vegetation and sites close to water (Sollmann et al. 2012). In contrast, pumas are considered habitat generalists and are less dependent on water sources (Logan and Sweanor 2001, Romero-Muñoz et al. 2010, Sollmann et al. 2012, Monroy-Vilchis and Soria-Díaz 2013, Gutiérrez-González and López-González 2017).

Other studies of overlapping temporal activity in populations of sympatric jaguars and pumas, noting that both felids can change their behavioral patterns when exposed to anthropogenic pressures such as agricultural burning, poaching, and logging (Scognamillo et al. 2003, Ávila-Nájera et al. 2016, Briones-Salas et al. 2016). Habitat use can also vary according to the level of human disturbance, mainly by the individual's selection of less-disturbed areas (Foster et al. 2010, 2013, Hernández-SaintMartín et al. 2013). Areas that are protected from logging, poaching, and other human-caused disturbance, and have high habitat heterogeneity allow for temporal and spatial niche segregation, which promotes coexistence (Scognamillo et al. 2003).

The Sierra Madre Oriental of northeastern Mexico represents one limit of the geographical distribution where jaguar and puma populations occur simultaneously (Vargas-Contreras and Hernández-Huerta 2001, Sunquist and Sunquist 2002). El Cielo Biosphere Reserve (ECBR) is located in the Sierra Madre Oriental and presents a well preserved high-diversity area due to low human impact, Nearctic and Neotropic convergence, extreme topographical conditions, and a large number of different habitat types (Steinberg et al. 2014). A previous study in ECBR described the temporal and spatial interactions of sympatric mesocarnivores (*Leopardus pardalis*, *L. wiedii*, and *Puma yagouaroundi*) and described their mechanisms of coexistence in time and space (Carrera-Treviño et al. 2018). These mechanisms are unknown for jaguars and pumas.

Given the variety of habitat types and the status of conservation of the ECBR, we hypothesized temporal and spatial segregation would be important mechanisms mediating the coexistence between jaguars and pumas. Our aim was to analyze temporal and spatial overlap between jaguars and pumas in the ECBR to help understand the segregation mechanisms that ensure their coexistence.

MATERIAL AND METHODS

Study site

We conducted our study in ECBR, which is in northeastern Mexico and is part of the state of Tamaulipas (Fig. 1). The ECBR has an area of 1, 445 km^2 and elevation ranges from 100 to 2, 300 m of altitude (Steinberg et al. 2014). Mean annual precipitation is 1000–2000 mm and mean annual temperatures are between 14 and 25.2 °C (INEGI 2013). The rainy season is from April to October and the dry season from November to March. The reserve is a site of Nearctic and Neotropical biogeographic zones of transition with high species richness (both faunal and floral) in a small geographic area (Steinberg et al. 2014). Habitat includes deciduous forest (DF), semi-deciduous forest (SDF), oak forest (OF), oak pine forest (OPF), mountain cloud forest (MCF), submontane scrub (SS), and others (Fig. 1, González-Medrano 2005, INEGI 2013, Steinberg et al. 2014). The reserve hosts an important mammalian biodiversity, including six felids' species: *Panthera onca*, *Puma concolor*, *Leopardus pardalis* (Linnaeus, 1758), *Leopardus wiedii* (Schinz, 1821), *Puma yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803), and *Lynx rufus* (Schreber, 1777); and the black bear, *Ursus americanus* (Pallas, 1780) (Vargas-Contreras and Hernández-Huerta 2001).

Sampling design

We established 26 study camera trap stations in five habitat types from January 2015 to December 2017. The mean distance between stations was approximately 6 ± 3 km. The number of stations in each habitat were chosen in proportion to the area of habitat it represented in the reserve: OF (414.6 km^2, n = 9 stations), DF (329.7 km^2, n = 8 stations), MCF (191.5 km^2, n = 5 stations), OPF (80.3 km^2, n = 2 stations), and SDF (69.6 km^2, n = 2 stations) (Fig. 1). These five habitat types cover 1,085.7 km^2, which represents 75% of the ECBR.

We installed two camera traps (Scoutguard HCO SG565) at each of the 26 sampling stations along unpaved roads and man-made trails to maximize the detection probability of jaguars and pumas (Goulart et al. 2009, Srbek-Araujo and Chiarello 2013). Camera traps were attached to tree trunks at 30–50 cm above ground, were active 24 hours and programmed to take one picture every 60 seconds. Date and time were also recorded in each photograph. We checked cameras monthly to make

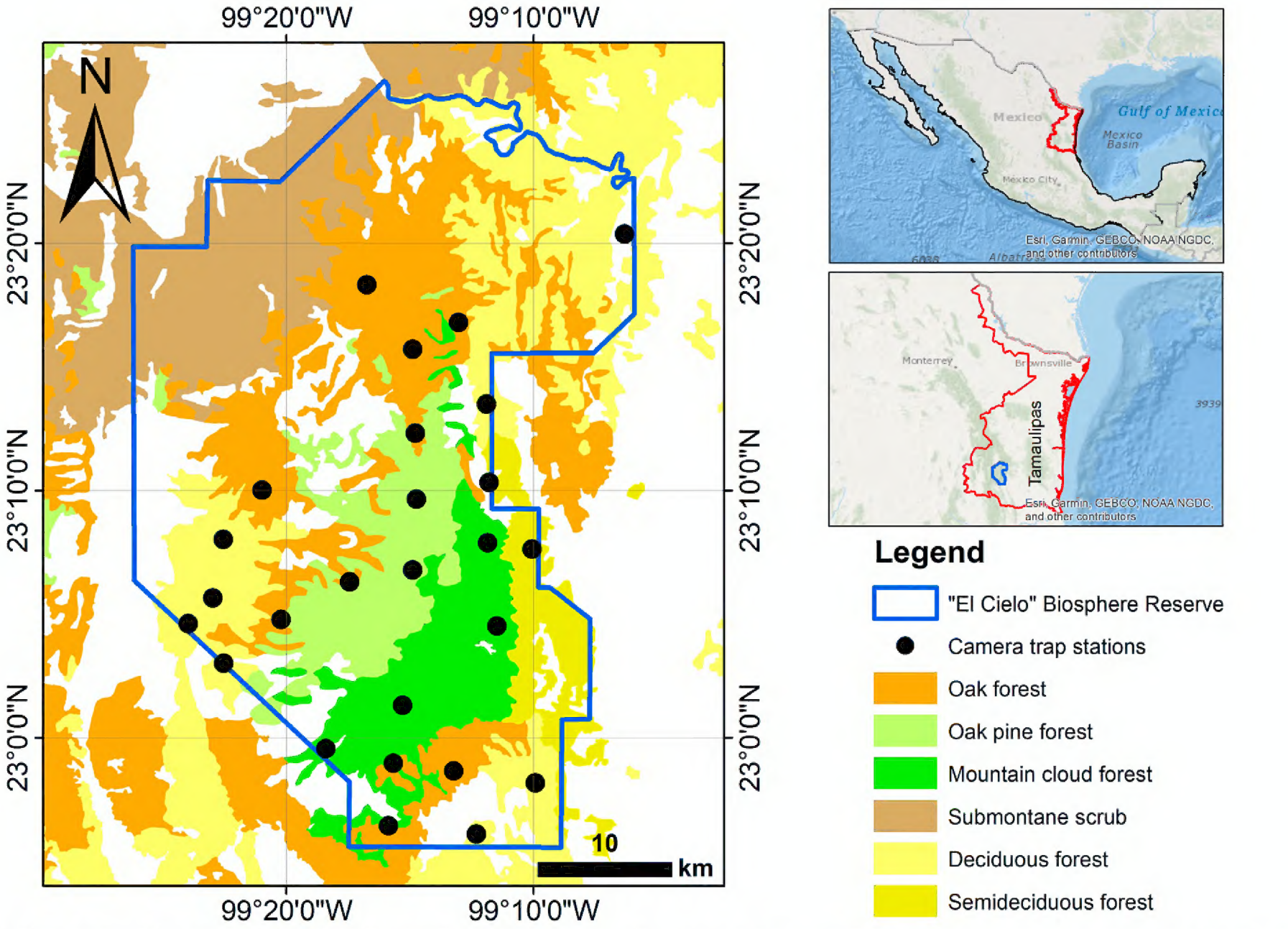

Figure 1. Geographical location of the El Cielo Biosphere Reserve in northeastern Mexico, with habitats and camera trap station locations.

sure they were working appropriately, replace batteries, and downloaded images from memory cards. No bait or lures were used during the study.

Photographs were classified as independent events to avoid autocorrelation. We define these independent events as: a) consecutive photographs of different individuals of the same species; b) consecutive photographs of individuals of different species; c) each individual in a group photograph; d) one hour between photographs only when it was not possible to identify individuals (O'Brien et al. 2003, Linkie and Ridout 2011).

Temporal activity

We grouped independent photographic events into 24 one-hour categories starting at 00:00 h. Daily activity patterns for each species were further broken down into day, night, and crepuscular (dawn and dusk). We determined the exact time of dawn and dusk by using Sun Times software v. 7.1 (Kay and Du Croz 2008, Carbajal-Borges et al. 2014), which considers the latitude and time zone of the ECBR. In this way, we calculated the range based on the monthly mean and considered one hour before and one hour after the corresponding dawn/dusk time (e.g. with a monthly mean of 07:45 h; range = 06:45–08:45 h for dawn, and with a mean of 19:44 h; our range = 18:44–20:44 h for dusk).

Temporal activity patterns for each species were analyzed using circular statistics implemented with the Oriana v. 4.02 software (Kovach Computing Services, UK). Rayleigh's Uniformity Test (Zar 2010, Sánchez et al. 2009) was used to verify whether the independent events of each species were non-randomly or uniformly distributed. Non-random timing of events could signal that the animals were nocturnal, diurnal or crepuscular. If independent events were uniformly distributed throughout the day, the species were classified as cathemeral (Zar 2010, Oliveira-Santos et al. 2012).

We also compared the activity pattern of the jaguar and puma between years (2015, 2016, and 2017) and seasons (dry and wet) using parametric or nonparametric circular tests depending on whether or not the data showed a von Mises distribution. This distribution can be regarded as the circular analogue of the normal distribution on the line (Forbes et al. 2010).

We calculated the temporal coefficient of overlap (Δ) and its 95% confidence interval from 10,000 bootstrap samples between jaguar and puma activity patterns (Ridout and Linkie 2009). The coefficient of overlap is defined as the area under the curve which is formed by taking the minimum of two kernel density indices (one

for jaguars, one for pumas) at each time point (Linkie and Ridout 2011). The kernel density index is used to estimate time use for each species by treating them as random samples from an underlying continuous distribution, instead of grouping photographic events into discrete time categories. Overlap values ranged from 0 (no overlap) to 1 (complete overlap). Low overlap was defined as $\Delta < 0.50$, moderate overlap was $0.50 < \Delta < 0.70$, and high overlap was $\Delta > 0.70$. Boundary values are intermediate to those of Massara et al. (2018) and are within estimated ranges from Monterroso et al. (2014). Time overlap analysis was conducted in R v. 0.3.3 using the overlap package (R Development Core Team; Meredith and Ridout 2020). Because we always had greater than 75 samples, we used the Dhat4 (Δ_4) estimator (Ridout and Linkie 2009).

Habitat use

We grouped independent events of jaguars and pumas into the five habitat types (DF, SDF, OF, OPF, MCF), and spatial overlap was subsequently calculated with the Pianka index. This index ranges from 0 (no overlap) to 1 (complete overlap) and was performed in EcoSim 7.0 software (http://www.garyentsminger.com/ecosim) (Entsminger 2014). We compared our observed overlap in the habitat between jaguars and pumas with null models of habitat overlap generated by EcoSim. Null models used 10,000 randomly generated interactions with a level of significance of 0.05. The RA3 algorithm was used because it preserves the specialization of each species but allows for the potential use of other resources (Winemiller and Pianka 1990, Gómez-Ortiz et al. 2019).

We also performed a selectivity habitat analysis to determine if the jaguars and pumas used or avoid some habitat types of the ECBR according to availability. We used satellite imagery (Google Earth) and ArcGIS 10.2 to digitize the five habitat types of the reserve and calculated the percentage of available area for each habitat (DF [30.37%], SDF [6.41%], OF [38.19%], OPF [7.40%], MCF [17.64%]). We used the index of selectivity (E_i) according to Krebs (1999): $E_i = (r_i - n_i)/(r_i + n_i)$, where r_i is the percentage of jaguar or puma in each habitat type i; n_i is the percentage of habitat type i available in ECBR. This index produces values from –1 (habitat avoidance) to +1 (habitat selection); values close to zero indicate habitat is being used according to its availability in the environment. The index data were resampled using bootstrap (10,000 replicates with replacement), 95% confidence intervals (CI) were estimated with R v. 3.1.3 (Glen et al. 2012), and means reported with ± 1 SD.

Further, to know on a fine scale if both felids share the same space, we determined the percentage of camera trap stations where jaguars and pumas were photographed at the same site, but at different times.

RESULTS

From January 2015 to December 2017, we had 28,220 camera trap days of survey effort and 1,063 photographs of jaguars and pumas, 553 of which were identified as independent events (371 jaguars; 182 pumas).

Temporal activity

The activity pattern of jaguars was mainly nocturnal; 80% of independent events at night and activity peaks at 21:00, 22:00, and 02:00 h (Fig. 2). The activity pattern of pumas was also nocturnal; 60% of independent events occurring at night

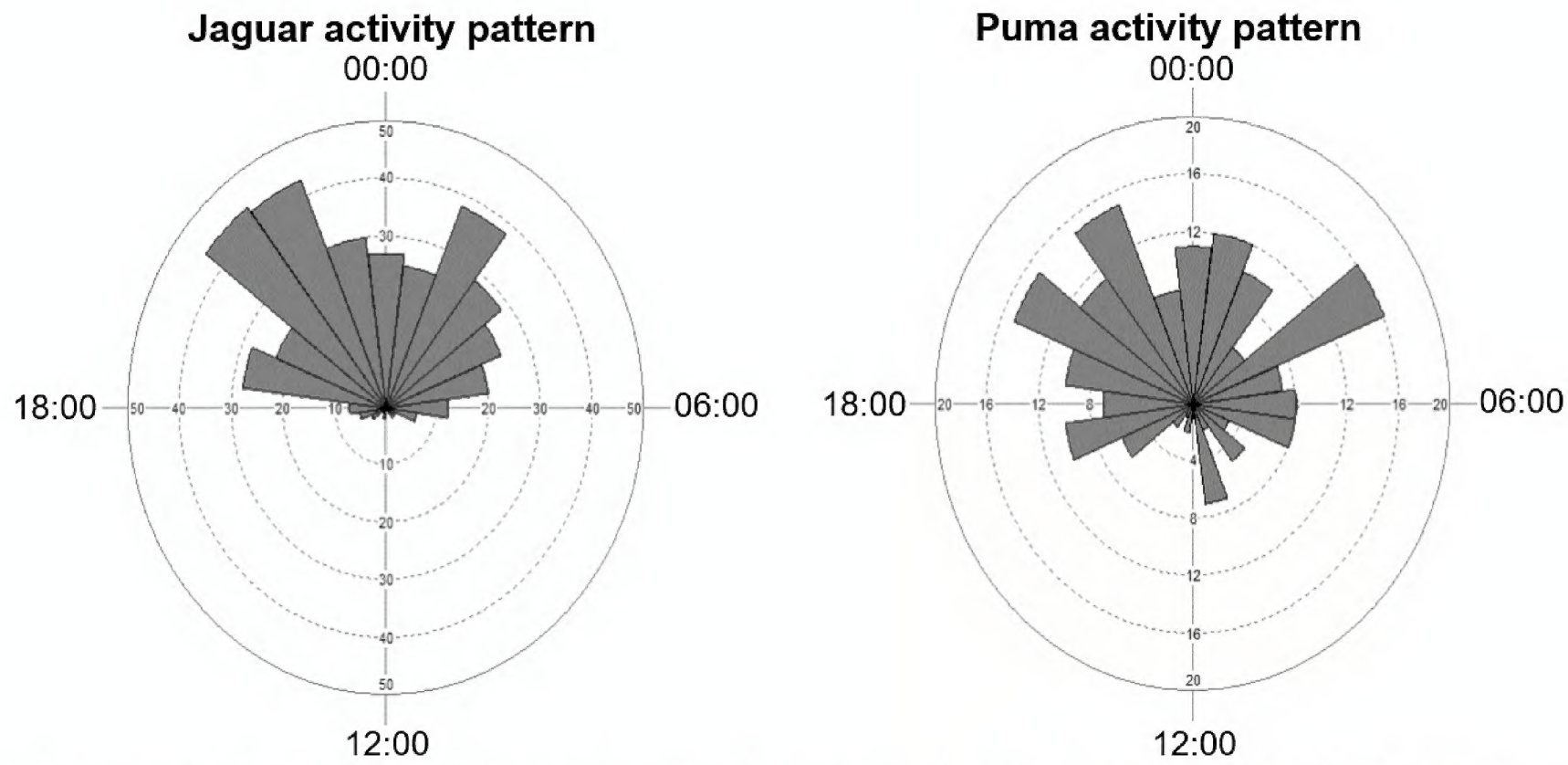

Figure 2. Circular histograms of activity patterns for jaguar (*Panthera onca*) and puma (*Puma concolor*) in El Cielo Biosphere Reserve, Tamaulipas, Mexico. Each bar is a discrete 1-hour time interval and is centered on the hour. The dependent variable (inner circles) is number of times jaguars or pumas appeared in photographs at each time interval.

activity peaks at 20:00, 22:00, and 04:00 h (Fig. 2). However, the rest of the independent events for pumas (40%) were distributed at different times during the day and we even observed puma activity peaks at 17:00, 06:00 and 07:00 h (Fig. 2). Rayleigh's Uniformity Test (Z) did not show a uniform distribution throughout the day in jaguars ($Z = 196.62$, $p < 0.01$) or pumas ($Z = 18.01$, $p < 0.05$), so neither species was classified as cathemeral (Zar 2010, Oliveira-Santos et al. 2012). In both species, the data showed a greater tendency toward nighttime activity (Fig. 2).

Jaguar and puma activity patterns did not show a Von Mises distribution (U^2) in some years (jaguar: 2015 $U^2 = 0.23$, $p < 0.05$; 2016 $U^2 = 0.04$, $p > 0.05$; 2017 $U^2 = 0.32$, $p < 0.05$; and puma: 2015 $U^2 = 0.05$, $p > 0.05$; 2016 $U^2 = 0.02$, $p > 0.05$; 2017 $U^2 = 0.03$, $p < 0.05$). Based on these results we use a Mardia-Watson-Wheeler (W) nonparametric multisample test to compare jaguar and puma activity patterns among sampling years, and no significant differences were found (jaguar: $W = 1.63$, $p > 0.05$; and puma: $W = 5.1$, $p > 0.05$).

We also compared the activity pattern of the jaguar between seasons (dry and wet) using the Watson-Williams (F) parametric test (two samples) and the Von Mises distribution (wet season: $U^2 = 0.41$, $p > 0.05$; dry $U^2 = 0.14$, $p > 0.05$). For pumas we use Mardian-Watson-Wheeler (W) nonparametric test (two samples), because the season did not show a Von Mises distribution (wet: $U^2 = 0.04$, $p < 0.05$; dry: $U^2 = 0.03$, $p < 0.05$). However, there were also no significant differences in activity between wet and dry seasons (jaguar: $F = 0.16$, $p > 0.05$; and puma $W = 0.89$, $p > 0.05$), so we did not consider those variables in the time overlap analysis.

Time overlap analysis showed a high coefficient of overlap between jaguars and pumas ($\Delta_4 = 0.77$) with confidence intervals of 0.71–0.84 (Fig. 3).

Habitat use

The habitat use analysis showed that jaguars mostly used DF with 90% of independent records found in this habitat types, while pumas mostly used three different types of habitats in ECBR: OF (35%), DF (31%), and OPF (24%). The Pianka index indicated an intermediate spatial overlap (0.61) between jaguars and pumas. Therefore, pumas show behaviors of a generalist species by using a greater number of habitat types, which is a potential strategy to avoid encounters with jaguars, and for both to coexist in the same landscape with similar habitats. We also recorded a low percentage (22.5%) of co-occurrence (sites where we photographed jaguars and pumas in the same space but at different times).

Habitat selectivity analysis (E_i) showed segregation in relation to habitat use. The jaguar selects the DF ($E_i = 0.48$), uses the SDF in proportion to availability ($E_i = -0.08$), and avoids using the MCF ($E_i = -1$), OF ($E_i = -0.84$), and OPF ($E_i = -0.39$). In comparison, puma prefers the OPF ($E_i = 0.41$), uses the OF ($E_i = -0.04$), DF ($E_i = 0.09$) and SDF ($E_i = -0.18$) in proportion to availability, and avoids using the MCF ($E_i = -0.51$). Based on the results of this analysis we believe that jaguars are more selective than pumas (Fig. 4) in their use of habitat and it is probably the main segregation mechanism that allows these felids to coexist in ECBR.

DISCUSSION

Jaguars and pumas are sympatric top predators across the entire jaguar range, share a remarkably similar morphology, and are obligate carnivores (Iriarte et al. 1990, Sunquist and Sunquist 2002, Haines 2006). Both specialize in mammalian prey and therefore experience significant intra guild competition.

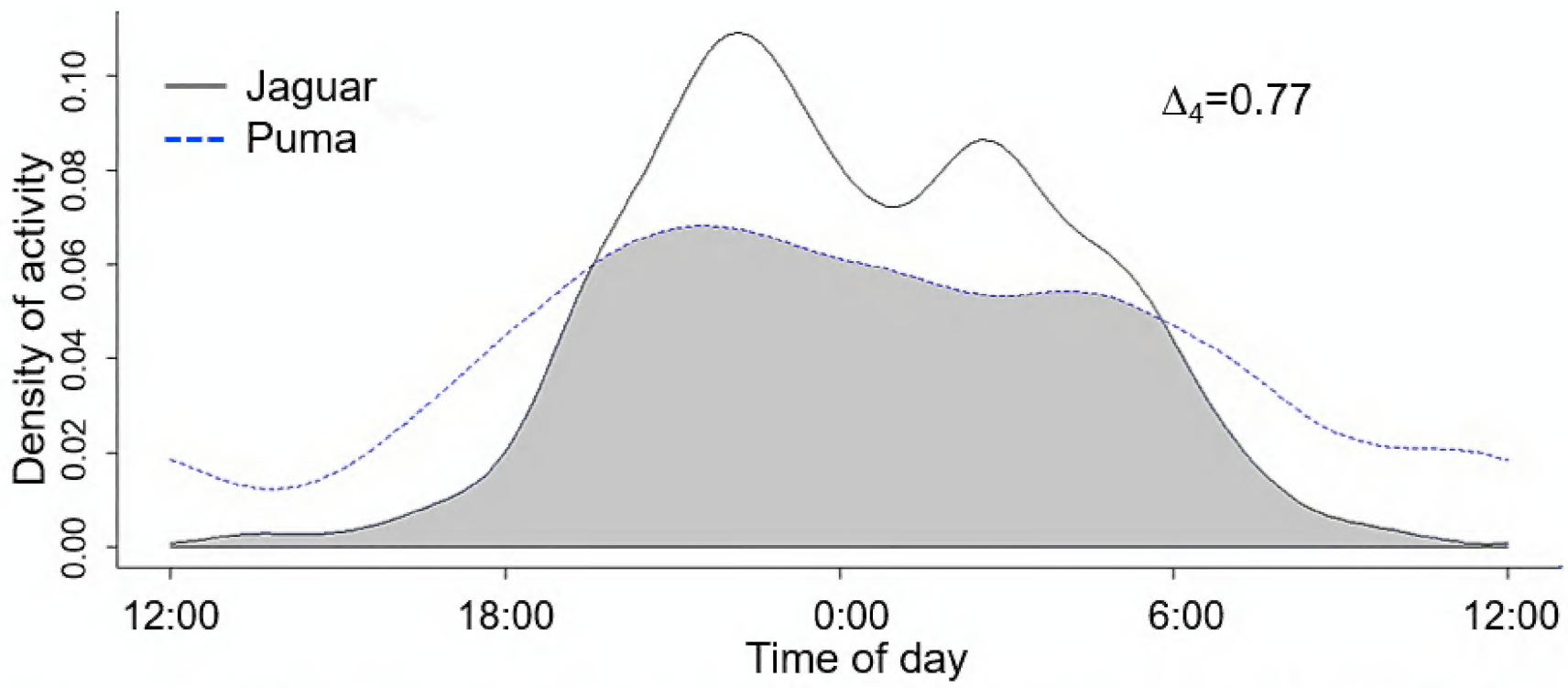

Figure 3. Time overlap analysis of activity patterns between jaguar (*Panthera onca*) and puma (*Puma concolor*) in El Cielo Biosphere Reserve. Time overlap is shown by the shaded area. The solid line represents the activity pattern of jaguars and dashed line shows the activity pattern of pumas ($\Delta_4 = 0.77$ is the result of the overlapping coefficient between jaguar and puma activity).

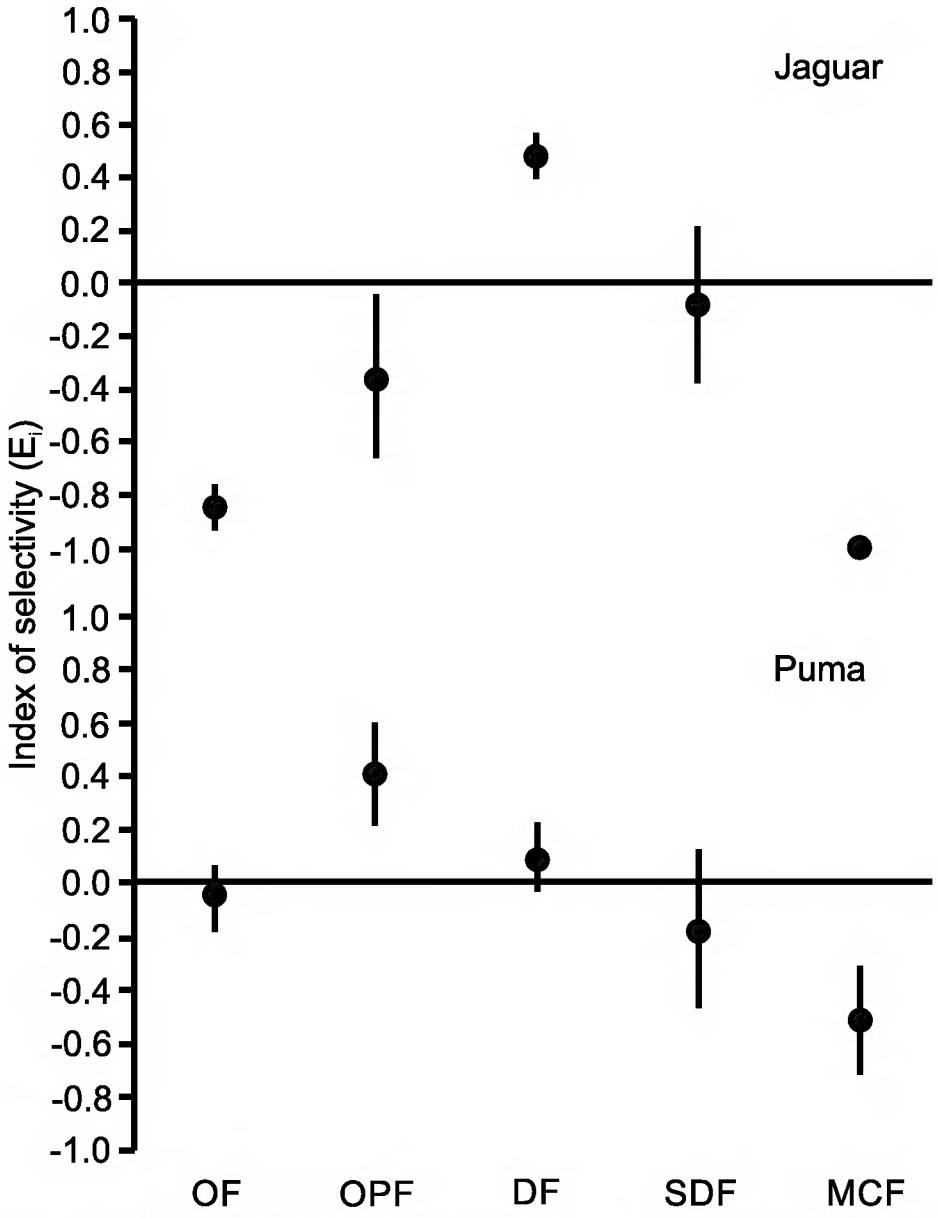

Figure 4. Habitat selection by jaguars and pumas based on the Index of selectivity (E_i) in El Cielo Biosphere Reserve, Tamaulipas, Mexico. (DF) Deciduous forest, (SDF) semi-deciduous forest, (OF) oak forest, (OPF) oak-pine forest, (MCF) mountain cloud forest.

Three axes of ecological niche (use of time, space, and food) are commonly used to decipher the intensity of interspecific and intraspecific interaction between species (Schoener 1974, Pianka 1978, Di Bitetti et al. 2010, Morato et al. 2016, Rayan and Linkie 2016). The theory predicts that high temporal overlap in these axes promote a high rate of competition between species. Low temporal overlap in one or more of the axes may signal a lower rate of competition, and thus species are more likely to coexist without significant negative effects on each other that could lead to the complete exclusion (Gause 1932, Hardin 1960).

Our results showed a high temporal overlap between jaguars and pumas in the ECBR ($\Delta_4 = 0.77$). These observations concur with results of studies conducted in the Venezuelan llanos (Scognamillo et al. 2003), Belizean rainforest (Harmsen et al. 2009), Quintana Roo, Mexico (Ávila-Nájera et al. 2016), San Luis Potosi, Mexico (Hernández-SaintMartín et al. 2013), and four Brazilian biomes (Foster et al. 2013). In the ECBR we think that pumas use two strategies of temporal activity, considering the argument that jaguars dominate pumas (Elbroch and Kusler 2018). 1) Pumas are active during daylight and crepuscular periods but increase their activity at night. 2) At night, when activity of both felids increases, some temporal segregation seems to be present. Jaguars are most active from 21:00 to 22:00 h, and 02:00 h, while puma activity peaks are in 20:00, 22:00 and 04:00 h (Fig. 2). However, based on these results (high temporal overlap), we believe that the temporal mechanism may only be a secondary strategy in the jaguar and puma interaction in ECBR. Some authors suggest that pumas adjust their activity pattern to local conditions on a finer scale as a strategy to avoid direct encounters and coexist with jaguars (Scognamillo et al. 2003, Moreno et al. 2006, Harmsen et al. 2009, Paviolo et al. 2009, Di Bitetti et al. 2010, Hernández-SaintMartín et al. 2013).

Jaguars were nocturnal in the ECBR (80% of the independent photographs) and did not show uniformity in their daily activity and were not considered cathemeral. The jaguar activity in this study is similar to that described in other studies (Rabinowitz and Nottingham 1986, Núñez et al. 2002, Maffei et al. 2004, Di Bitetti et al. 2010, Foster et al. 2013, Carrera-Treviño et al. 2016, De la Torre et al. 2017) but differs from some that classify them as cathemeral (being active throughout day) (Emmons 1987, Gómez et al. 2005, Blake et al. 2012, Hernández-SaintMartín et al. 2013).

Pumas showed a greater tendency to be nocturnal but showed activity at different times throughout the day; however, were not considered cathemeral. Other authors mention that puma activity during the day is common and may be due to low human activity and the availability of prey during the day (Núñez et al. 2002, Scognamillo et al. 2003, Paviolo et al. 2009, Di Bitetti et al. 2010, Hernández-SaintMartín et al. 2013, Ávila-Nájera et al. 2016, De la Torre et al. 2017). It's possible that the activity shown by pumas during the day in the ECBR is due to the presence of the jaguar and minimal human activity. Carrera-Treviño et al. (2016) reported no sightings of pumas during daylight hours on the periphery of the ECBR probably because their study was carried out in disturbed areas and those with human settlements.

The reasons for nocturnal activity of jaguars and pumas are variable, but some authors hypothesize that hunting at night is advantageous because the two felids can get closer to their prey without being detected (Sunquist and Sunquist 2002, Estrada-Hernández 2008), prey are more detectable or vulnerable at night (Emmons 1987, Sunquist and Sunquist 2002), and cool nights allow felids to spend less energy hunting or when moving from one place to another (Sunquist and Sunquist 2002, Estrada-Hernández 2008, Foster et al. 2013).

Understanding how large felids use habitat is essential to allow us to identify whether habitat use is a strategy for coexistence in species that are potential competitors (Cristescu et al. 2013). Our results of spatial overlap showed an intermediate overlap between jaguars and pumas (Pianka index = 0.61). Habitat use analysis showed that the jaguar prefers DF, uses SDF in proportion to availability and avoids the MCF, OF and OPF. In comparison pumas prefer OPF, also had records in OF, DF

and SDF, and used these types of vegetation according to their availability and avoids the MCF (Fig. 4). Thus, it is possible that jaguars are more selective in their use of habitat than pumas in the ECBR. Other researchers argue as well that the pumas are generalists and can be found in a wider range of habitats than the jaguar across their distribution (Iriarte et al. 1990, Sunquist and Sunquist 2002). Pumas can even live in proximity to humans (Dickson and Beier 2007, De Angelo et al. 2011, Sollmann et al. 2012), but they sometimes also avoid areas disturbed by human activity (Paviolo et al. 2009, Di Bitetti et al. 2010, Foster et al. 2010, De Angelo et al. 2011). Finally, the low percentage of co-occurrence (22.5%) in sites where jaguars and pumas were photographed using the same space at different times may indicate they actively try to avoid each other. Scognamillo et al. (2003) suggest that differences in use of habitat patches by jaguars and pumas in the Venezuelan llanos was an important component of their ecological separation.

Based on our results of spatial overlap (Pianka index = 0.61), habitat use, and low percentage of co-occurrence in shared sites, we believe this is the mechanism that best explains the coexistence of jaguars and pumas in ECBR. Of course, this statement should be taken with caution until the diet of these two felids can be analyzed in a future study. Jaguars showed a strong preference for DF, used three other habitats sparingly, and were absent from the MCF. Pumas preferred OPF but used the four other types of habitats (albeit some sparingly). Because of the ECBR's variety of habitat types, high heterogeneity, and low disturbance by humans (Steinberg et al. 2014), jaguars and pumas are able to avoid each other and coexist. Other authors have suggested that in heterogeneous landscapes two sympatric carnivores can use different habitat types to coexist and it is known that pumas use a wider range of habitat than jaguars (Emmons 1987, Aranda and Sánchez-Cordero 1996, Johnson et al. 1996, Scognamillo et al. 2003, Sollmann et al. 2012).

Additionally, Elbroch and Kusler (2018) analyzed whether pumas are dominant, subordinate, or equal to other apex predators, and conclude that jaguars are the dominant species over pumas (60%). Generally, pumas tend to change their activity pattern, habitat, and diet to avoid competing with the jaguar. However, other studies have identify situations where jaguar is not a dominant over the puma, although these studies were completed in areas where the pumas are more abundant than jaguars and the environment is more favorable to pumas (arid environment) (Romero-Muñoz et al. 2010, Ávila-Nájera et al. 2016, Gutiérrez-González and López-González 2017). In this regard, our results point to that, in ECBR, these felids avoided each other, and the puma is probably subordinate and less abundant, because: 1) The ECBR is located in a humid tropical environment (Steinberg et al. 2014), which is favorable for the jaguar; 2) Jaguars had more independent photographs (371) than pumas (182), which may be an indicator of greater abundance; 3) Pumas were active in daylight and during crepuscular hours, as well as using some night time hours, while jaguars were almost exclusively nocturnal; 4) Pumas used four habitat types; 5) We recorded a low percentage of co-occurrence (22.5%) in sites where pumas and jaguars shared the same space.

Our results yielded interesting conclusions of temporal and spatial interactions between jaguars and pumas and improves our knowledge about the ecology of these Neotropical felids within a protected area (ECBR). We suggest that temporal segregation is not the main coexistence mechanism between these two felids because our temporal overlap results were high. Temporal segregation may only be a secondary strategy in the jaguar and puma interaction. Instead, we suggest that spatial segregation may be the mechanism that best explains the coexistence of the jaguar and puma in the ECBR. We believe that the presence of different habitat types allows these felids to avoid each other and coexist. In addition, the puma's generalist habits are an important factor to consider. In this study, pumas used a wider array of time and space. Finally, we recommend in a future study in ECBR, to determine the diet of the jaguar and puma (scats analysis) to include an analysis of trophic niche overlap between those two felids, and then, analyze the temporal overlap of the felids and their main prey. This last analysis is essential, because it would help to corroborate the coexistence of the jaguar and puma in the ECBR.

ACKNOWLEDGEMENTS

We thank the Programa para la Conservación de Especies en Riesgo de la Comisión Nacional de Áreas Naturales Protegidas (CONANP); the owner of the lands, and volunteers of the wildlife laboratory of the Faculty of Veterinary Medicine and Zootechnics of the Autonomous University of Nuevo Leon, Mexico. We also thank the Autonomous University of Tamaulipas for funding the project UAT/PFI2015-15, and to the Program for Professional Development for Higher Education (PRODEP) through the project UAT-PTC-221/511-6/17-8212. We also thank to two anonymous reviewers for their comments and to R.J. Smith for copyediting English version.

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Submitted: January 17, 2021
Accepted: June 10, 2021
Available online: June 25, 2021
Editorial responsibility: Jorge Salazar-Bravo

Author Contributions: LSD and RCT contributed to the original idea; CACD, CCAS, YGO and LSD wrote the draft of the manuscript; RCT, LMG, CACD and LSD designed and conducted the sampling; YGO, JCCH and CCAS, analyzed data and provided revision on the manuscript.
Competing Interests: The authors have declared that no competing interests exist.
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